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# RECENT RESEARCHES UPON THE SUCCESSION OF THE TEETH IN MAMMALS.

BY HENRY FAIRFIELD OSBORN.

While American paleontologists have been making rapid advances in the phylogenetic history of mammalian teeth, the English have made notable additions to our comparative anatomical knowledge, and the Germans to the embryogenesis. The recent studies of Kükenthal, Röse and Taeker in the discovery of the complete double or milk dentition in the Marsupials, and in the discussion of its relation to that of the reptiles, also in the ontogenesis of the crowns of the teeth among the Cetaceans, Edentates, Primates and Ungulates are of the greatest interest and importance. They involve a complete revolution in our ideas as to the interpretation of the dentition in the three orders first mentioned above.

The latter authors are perhaps inclined to lay too great stress upon the testimony of ontogenesis in the order of appearance and consequent homologies of the mammalian cusps, and Röse's work is to a certain extent rendered less useful by the fact that he has substituted the conclusions of ontogeny for those based upon the more certain foundations of phylogeny. It is a subject of congratulation, however, that these authors, who constitute the rising school in Germany, recognize the value of the paleontological work done in this country, and are ready to join hands in pushing forward these investigations upon a joint basis.

## KÜKENTHAL'S RESEARCHES.

Kükenthal's studies upon toothed whales were partly directed upon the theory of Weber, Julin and others that these animals were formerly heterodont. In the embryo of the Porpoise (*Phocœna communis*,) he found traces of a heterodont condition quite sharply marked. There were twenty-five teeth in each half of the jaw, and the posterior seven were found to have two or three cusps. Having thus supported the opinion that the homodont toothed whales were primitively heterodont, Kükenthal has also proved that they are diphyodont, and that the dentition of the toothed whales is a true milk dentition, while the second or permanent dentition is represented by rudiments which display a distinct crown of enamel and even the enamel pulp, yet does not reach the surface.

In the whalebone whales in which germs of teeth had been found in the first third of foetal life, Kükenthal does not confirm the opinion of Weber that the dentition is heterodont. He denies that the posterior teeth are more complex than the nine anterior teeth, and holds that throughout they are simply conical, excepting in cases where two external teeth are fused together. This fusion of teeth does not follow any definite rule; in some cases it occurs in the anterior nine teeth. The course of embryonic development shows that these fused teeth represent an original condition, and in the opinion of the author, are to be regarded as molars. This conclusion was reached by the comparison of younger and older embryos, the number of fused teeth constantly diminishing in the latter.

Kükenthal advances the hypothesis that this was the method by which numerous homodont teeth arose from a small number of heterodont, namely, by the splitting apart of cusps. This hypothesis he promises to support by paleontological evidence. He also shows that these embryonic teeth in the whalebone whales also represent the first or milk dentition; and that the rudiments of a second series of teeth develop beneath them. Kükenthal refers these transformations in the dentition to natural selection, terminating with diminished calcification connected with the advantage of diminished specific gravity.

His general conclusions are, that all the earliest mammals were diphyodont. This is based upon his discovery of successional teeth in Marsupials, Edentates, Odontocetes and Mystacocetes. The monophyodont and homodont condition of many mammals, such as the toothed whales, he believes has been secondarily acquired. Within the higher members of the mammalian class the second dentition is developed progressively, both as regards form and function; while in the lower divisions, the first or milk dentition is predominant. "In the rudimentary stage both dentitions are of equal value. Embryology gives us no support for the often expressed assertion, that one of the two dental rudiments has arisen in dependence upon the other. They are both sisters, whose mother is the simple invagination in the jaw, which we term the dental fold, (*Zahnleiste.*)" He continues, that there are no absolute differences between mammalian and reptilian teeth; that not one of the characters of the mammalian teeth is perfectly constant, and that the derivation of the dentition of mammals from that of the reptiles does not appear to be too hazardous. Of the several series of teeth which are found in reptiles, only two persist in the mammals.

From this I would dissent in part. The three differences between the mammalian and the reptilian teeth are shown in the capacity for the multiplication of cusps upon the crown, in the division of the fang whenever the crown becomes multicuspid, in the acquisition of the cingulum. The frequent succession of teeth in the reptiles, may be the cause of the non-progression of reptilian as compared with mammalian teeth. In the reptilia among the Theromorpha, we find true triconodont crowns, as for example in *Galesaurus*, and a heterodont dentition which closely imitates that of the mammals; but the class differences appear in the fact that in the mammalia a development of lateral cusps upon the protocone, and the stages from the protodont toward the triconodont type, are marked step by step by the division of the fang. This law was advanced hypothetically by Cope and Wortman, and I regard it as absolutely proven by the evidence I have adduced in the study of *Dromotherium, Microconodon* and *Amphilestes.*

The hypothesis of Kükenthal and Röse that the numerous single pointed or homodont teeth of the whales, have arisen by the splitting up of the three cusps of a triconodont crown is an ingenious one, upon which paleontology at present throws no favorable light. *Amphilestes* of the middle Triassic with its seven triconodont molars, might by such a splitting process, furnish twenty-one homodont teeth; nevertheless this seems to me highly improbable; while the converse hypothesis suggested by Kükenthal and developed by Röse, that multicuspid crowns have originated by the fusion of single cusps, is capable of direct disproof by paleontological evidence.

The multiplication of teeth accompanying the elongation of the jaw in Cetacea, can be much more simply explained by the supposition that the dental fold was carried backward, and gave rise to new teeth caps at definite intervals. I may add that the rapid reduction of the molars in the Mesozoic period from behind forward, which reduced their number in the *Triconodontidæ* from seven to four, between the middle and upper Jurassic periods, is against the supposition that the *Amphilestes* molar, for example, furnished the material for the multiple Cetacean series.

Kükenthal's researches upon the dentition of the opossum, published in 1891,[1] mark another great step in advance in our knowledge of the dentition of the mammals. We may refer to the later researches of Röse for details, and simply quote one passage from Kükenthal:

"The permanent dentition of the Marsupials, belongs to the first series or milk dentition. Rudiments of the second dentition are actually present in an embryonic condition, but with the exception of the third premolar, they do not cut the gum." Again, the two first so-called true molars, of the upper jaw, and the first three similar teeth of the lower jaw, also belong to the first dentition and have rudimentary successors. Therefore, excepting the last upper and lower molars which appear at a late stage of development, neither dentition of *Didelphys* belongs to the so-called permanent series. This opinion has been somewhat emended by Röse.

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[1] Anatomischer Anzeiger, Nos. 23, 24.

## RÖSE'S RESEARCHES.

MARSUPIALS. Dr. Röse gives the following summary of his principal results. "When we combine the results of the foregoing researches, we find that the development of the teeth in the Marsupials follows exactly the same principle as that of man and the other mammalia. The first matrix is indicated by the dental fold, i. e. a part of the epithelium of the jaw which grows into the mesoderm aided by an extensive fold. Upon this dental fold are formed the dental caps which belong to the first series; in the case of *Didelphys*, the incisors, the canine, two premolars and the first molar. These dental caps are then immediately constricted off from the dental fold, and this ridge grows both inwards below the dental caps, and backwards behind the molar above mentioned. The posterior molars arise in exactly the same manner as I have described; in the case of man, through lateral extension of the dental ridge.

"While, however, in the case of man, the permanent ridge extends beneath the ten anterior teeth constituting the milk series and gives origin to ten permanent teeth, which cause their predecessors to be absorbed, in the Marsupials only the last premolar of the adult arises from the dental ridge of the permanent teeth. It is nevertheless, more than probable that the outer (5th) incisors of *Perameles*, as well as of Macropus and Phalangista, are built up from the permanent ridge, i. e. they belong to the second dental series. The last upper premolar belonging to the second series in some cases simply pushes its way into a gap in the first series without causing the usual absorption of the first tooth in this row. This type we find to be shown in *Didelphys*, in *Perameles*, in *Phalangista cookii*, as well as in *Macropus.* In other cases the last premolar of the first series is absorbed, and in its place enters the premolar of the second series; this more primitive type is found in an undetermined species of the genus Phalangista; also in *Macropus lugens* and *M. gigantius*; also, according to the figures of Oldfield Thomas, in *Phascogale,* and in the fossil *Triacanthodon serrula.*

" Further researches are necessary to determine which type is the most common among the Marsupials. It also remains to ascertain through sections and models, whether the last incisor (fifth or lateral, $i^5$) of the upper jaw really arises from the second series, and in what species this occurs. Possibly in some Marsupials other teeth also rise from the second series. Whether this, however, is the case or not, the principal theory of Marsupial dentition is not thereby affected. It is certainly well established by my researches, as well as by those of Kükenthal, that the teeth of the Marsupials, with the exception of the last premolar and probably of the last superior incisor of some species, belong to the first series, and are analogous with the milk teeth of man and other mammalia.

"This shows that in the entire vertebrate series the principle holds good, that by the better development of the single tooth, the frequent succession of teeth of the Selachian type, is gradually limited. The Marsupials, however, in the reduction of the multiple succession of the reptilian-like ancestors of existing mammals, have together gone past the limit, and have wandered into a *cul de sac* of evolution out of which there was no return. Upon this rests the remarkable constancy of this order, from the Mesozoic period to the present time. The reduction of the former multiple succession of teeth of the vetrebates to a single series of teeth, appears therefore, only to be of service when the teeth at the same time attain a permanent growth. This stage was only attained among the Marsupials by *Phascolomys.*"

In the same paper the author restates his theory of the origin of premolars and molars by the fusion of several single teeth, and is led far astray from the actual conditions which we observe in such development. Originally, he says, the premolars, like the molars, embraced three single cusps, which were arranged in the triconodont type; in Triacanthodon the premolars are altogether formed like the molars. (This observation is an error. The only Mesozoic mammal in which the premolars are even approximately similar to the molars, is *Phascolotherium.*) After the original three cusps of the premolars had been arranged in the triconodont order, he supposes, arose the degeneration of the forward cusp, leaving a tooth type which we observe especially among the Carnivora. (The cusps left here are simply the protocone and talon.)

In an earlier paper upon human dentition, the author is also led astray by ontogeny to false conclusions as to phylogeny, and at the conclusion of his extremely interesting paper upon the embryogenesis of the human dentition, he says: "The typical form of upper molars in man is unquestionably the four cusped type; while the typical form in the lower molars is the five cusped type."

EDENTATES. Dr. Röse has also contributed interesting observations upon the rudimentary development of teeth among the Edentata. He quotes Max Weber to the effect, that the reduction of the teeth in *Manis* is so absolute, that not a single rudiment remains, and that there is, so to speak, no place left for the layer either of dentine or enamel. He then goes on to say: "After, in my earlier studies, I recognized the morphological importance of the dental fold, and finding it ended as a last rudiment of an earlier dentition both in the birds and turtles, I did not doubt that also in *Manis,* at least the first stages of a dental ridge must be present in the early embryonic development." With material received from Professor Max Weber himself, Dr. Röse demonstrates the beginnings of the dental fold both in the upper and lower jaws of Manis; and in the lower jaw on both sides he finds even an unmistakable rudiment of the tooth layer, in the form of a swollen portion of the common dental fold, i. e. an abortive tooth cap. Such results were obtained in *Manis javanica.*

The forms investigated were the Nine-banded Armadillo (*Dasypus novemcinctus*), *Dasypus hybridus,* the Pangolin (*Manis javanica*), and the Anteater (*Myrmecophaga.*) In the Nine-banded Armadillo most careful researches were made upon the dental ridge in a series of 420 sections, leading to a discovery which was confirmed in the other species, that the dentition of the Edentata has arisen by degeneration from the dentition of a more highly organized mammalian type. This result is directly contradictory to the hypothesis of Oldfield Thomas, that the Edentata were sharply marked off as *Paratheria* by the exceptionally simple features of their dentition among other characters.

Dr. Röse continues, that the enamel of the teeth has so far retrogressed, that only an upper capping of the enamel layer is formed, which lies directly upon the dentine. "In all cases in which we have instituted exact microscopical researches, in three species of Dasypus, and in Orycteropus, it is proved that invariably in the Edentata the typical two dentitions of the mammalia are exhibited in the embryonic stages. In every case as the tooth is constricted off, the dental ridge grows further backwards, as the basis of the successional tooth, as it has been observed in the development of the teeth in man and in the Opossum; and as Kükenthal observes, from a morphological standpoint it is of no moment whether this replacing ridge gives rise to teeth or not."

Dr. Röse anticipates that the Bradypodidæ will also prove to be diphyodont.

This author further shows that there are proofs of heterodonty which weigh against the opinions of Parker and Thomas, that the Edentata stand entirely aside from the other mammalia.

In the early stages of development, a continuous dental ridge is found in the whole jaw, and in the anterior part of the jaw two rudimentary teeth are observed which must be regarded as incisors. According to Rheinhardt, the number of rudimentary incisors in the Nine-banded Armadillo is still greater (four). The lateral tooth in Bradypus may be either an incisor or canine. Dr. Röse agrees with Tomes and Osborn that the canine should be considered as the most anterior premolar. Another question arises as to whether the posterior teeth of the Edentata are to be regarded as molars or as divided into molars and premolars. As Kükenthal has observed in the whalebone whale, we also find in young embryos of the Edentates a double pointed or biconodont tooth, which later divides secondarily into its single pointed components. The author considers it doubtful whether this biconodont type is primitive, or as seems to him more probable, is derived by degeneration from a triconodont type!

As regards the bearing of paleontology and comparative anatomy upon these facts, we find rudimentary incisors in the living *Dasypus setosus* and in the fossil *Chlamydotherium.* The latter shows the fusion of two conical points. The author refers also to Glyptodon, which has prismatic back teeth with a very evident triconodont type. He concludes by saying that these circumstances afford a very marked support for the opinion, that the present biconodont teeth of these Edentata, at least the posterior members of the series, have arisen by reduction of a typical triconodont type. If this is confirmed by further observation, it will be a fact of the very greatest importance in the phylogeny of the mammalia. For the triconodont type has been shown to prevail in the upper Triassic and lower Jurassic periods. There was unquestionably a vast period in the evolution of mammalia in which a triconodont molar was the only type.

SAUROPSIDA. In the conclusion of his work upon the development of the teeth in the crocodile, he reaches the following result: " The cause of the existence of the thecodont (fangless) teeth is to be found in the continuous growth of the epithelial sheath of Hertwig. . . . . . . . The functional tooth of the crocodile is altogether analogous with a rooted mammalian tooth, the growth of which is not yet complete. The first embryonic tooth series of the crocodile, on the other hand, exhibits a development which we hitherto have only observed in the Selachia and Urodela through the labors of Hertwig. The theory of Hertwig as to the genesis of the mouth skeleton out of the cement sockets of tooth structure, has received an unexpected and weighty support by our researches."

The types examined by the author, included *Sterna Wilsonii,* the Ostrich, *Struthio camelus* and the turtle, *Chelone* *midas.* He anticipated from his studies upon the tooth development of the reptiles, that only traces of the dental fold would be found, and if any really rudimentary dentine teeth were found, they could only represent those primitive Selachian-like teeth which constitute the first series of the crocodile. In the crocodile as above noted, a first dental layer exhibits itself altogether similar to the placoid scales and the first teeth of the Selachians in the form of free papillæ upon the surface epithelium of the jaw.

## TAEKER'S RESEARCHES.

Dr. Taeker of the Veterinary Institute of Dorpat, has completed a most interesting series of studies upon the embryonic form of the teeth in the Ungulates.

His technical methods were an improvement on those introduced by Klever, and his material included embryos of the horse as a type of the most complex form of perrissodactyl, of the pig as a modern bunodont, and of Selenodonts he selected the embryos of the Elk, Deer, Ox and Sheep, and of greater rarity, an embryo of one of the group of Tragulids. His conclusions are summed up as follows:

1. As a result of my investigations I find that both the Suidæ with rounded or bunodont cusps, and the Ruminants with their crescentic or selenodont cusps, arise from a similar initial bunodont stage; that is, all the highly complex forms of modern cusps spring from the simple ancestral hillock in the embryonic stages.
2. The order of differentiation soon follows, in which the separate cones and conids (cusps of the lower jaw) are transformed into pyramids in the case of the pig, and into crescents in the case of the ruminants.
3. The transformation of the cones is not effected simultaneously, but successively. In the upper teeth it does not begin with the protocone (antero-internal cusp which is first developed in the paleontological history), but with the external cusps, the paracone and metacone.

*Order of Appearance of the Cusps.* The author observes that while in the lower jaw the order and appearance of the cusps is the same in the embryo as in the paleontological history, in the upper jaw this ontogenesis is no longer parallel with phylogenesis, (as regards the upper teeth, this exception is confirmed by Röse). In fact the external cusps not only appear before the internal cusp, which paleontology shows to be more primitive but they assume the crescentic form earlier. In other words, their development is accelerated.

The development of the premolars is also traced and it is interesting to recall the fact that in the paleontological history, the order of evolution of the cusps of the premolars is not the same as that of the molars. Taeker's results therefore show a parallelism between Ontogenesis and Phylogenesis, in that he proves that the embryonic cusp order in the premolars is different from that in the molars, and is approximately similar to that in the ancestral history as recently worked out by Scott.

Upon the whole this parallelism between embryogenesis and palingenesis is most striking, and I think we can explain the exceptions which Taeker and Röse have shown to occur in the upper teeth both in the Primates and Ungulates, in the following manner: In the most primitive types of trituberculates, the protocone was the most prominent cusp in both jaws. This is seen in all the known Triassic and Jurassic trituberculates without exception. During the Cretaceous period a change took place, in which the upper molars rapidly diverged in pattern from the lower molars. The lower were more conservative, retaining the trigonid or triangle in its primitive proportions. The upper molars, on the other hand, must have undergone a marked change, consisting mainly in the depression of the protocone below or to the level of the paracone and metacone, as seen in the primitive Carnivores, Creodonts, and Insectivores of the Puerco period. Thus we find both in the Ungulates and sub-Ungulates or early Primates, that in the upper molars the outer two cusps are slightly more elevated and decidedly more progressive in the acquisition of new forms than the older internal protocone. For example the outer cusps often became crescentic, while the inner cusp remained rounded. And it was therefore during all the lower Eocene, that the external cusps surpassed the internal cusps in progressive development.

The bearing of these facts is this: in Embryogenesis, we are dealing with repetition of ancestral history; we should not expect, however, that this repetition would invariably extend back of the form characteristic of the Eocene period. As a matter of fact, the upper molars repeat their Eocene but not their Mesozoic form. The lower molars also repeat the Eocene form, and this, as explained above, owing to the conservative proportions of the cusps, is also the Mesozoic form, the protocone still being the most prominent cusp in the crown. While, perhaps, not thoroughly satisfactory, there is a great deal of probability that the discrepancy between the embryonic and phyletic order in the upper molars, is due to these differences in their phyletic history.

In the accompanying table I have summed up the phylogenetic order observed by Cope and myself, and the ontogenetic order observed by Röse and Taeker.

## THE FUSION THEORY OF CUSP ORIGIN.

As we have seen, the fusion theory was first proposed by Kükenthal; it was afterward independently advanced by Röse. We find in addition to the grounds given above, one very strong argument against this theory derived from Paleontology, is in the law of molar evolution, namely, that the cusps appear at or near the apex of the crown, and development takes place from above downward. Thus, so far as we can judge from *Dromotherium* and *Microconodon*, the lateral cusps first appear on the sides of the protocone, and much later, the fang subdivides; the lateral cusps are at the outset very much smaller than the medium cusp, and it is only after a long course of evolution that they attain the same size.

Now, if the fusion theory were correct, and the triconodont crown, for example, were constituted by the fusion of three

## Table showing the Phylogenetic Order as observed by COPE and OSBORN, and the Ontogenetic Order as observed by RÖSE and TAEKER.

| A. Phylogenetic Order. | | | | B. Ontogenetic Order. | | | |
|---|---|---|---|---|---|---|---|
| Geological Periods | Order. | Cusps Comparative—Human.) | | Primates 2) | Marsupials 2) | Ungulates 3) | Order. |
| | | **Upper molars.** | | | | | |
| Permian | 1 | Protocone | Ant. lingual. | Paracone | Paracone | Paracone | 1 |
| Triassic & Jurassic | 2 & 3 | Paracone | " lateral. | Protocone | Proto- " | Meta- " | 2 |
| | | Metacone | Post " | Metacone | Meta- " | Proto- " | 3 |
| Cretaceous | — | | | | | | |
| Eocene & Miocene | 4 | Hypocone | Post. lingual. | Hypocone | Hypo- " | Hypo- " | 4 |
| | | **Lower molars.** | | | | | |
| Permian | 1 | Protoconid | Ant. lateral. | Protoconid | Protoconid | Protoconid | 1 |
| Triassic & Jurassic | 2 & 3 | Paraconid | (degenerated 1)) | Metaconid | Para- " | Meta- " | 2 |
| | | Metaconid | Ant. lingual | Hypoconid | Hypo- " | Hypo- " | 3 |
| Jurassic | 4 | Hypoconid | Post. lateral | Entoconid | Ento- " | Ento- " | 4 |
| Cretaceous | 5 | Entoconid | " lingual | Hypoconulid | Meta- " | | 5 |
| Lower Eocene | 6 | Hypoconulid | " mesial | | | | |

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1) This cusp degenerates both in the early Primates and Ungulates.
2) As I understand Dr. RÖSE.
3) As I understand Dr. TAEKER.

distinct cones, these cones should certainly appear sub-equal from the first, and they should present a division extending to the base and indicated in the fang. From the fact that Kükenthal does not mention the above genera, we infer that his attention has not been called to them. In one of his latest addresses he speaks as if the multituberculates were the only Triassic mammals. We know that the trituberculates were as old or older than the multituberculates, and reasoning by analogy, I have attempted to show elsewhere that the multituberculates will be found to have a trituberculate origin.

As I have lately criticised this theory in some detail in the "Anatomischer Anzeiger," I here refer to the well-known evidence which renders the Kükenthal-Röse hypothesis both superfluous and untenable; when we find in the series such as is represented by the genera Dromotherium, Microconodon, Spalacotherium, Amphitherium, Miacis, exhibiting in the lower jaw all the stages between the sectorial and bunodont crown, and when in the early Ungulates we are able to trace one by one the successive additions of cusps to the bunodont molar, often in the center of the crown, it certainly is not necessary to attempt to establish any new hypothesis as to cusp origin.

## SUMMARY OF RESULTS.

The general bearing of these researches upon the stem forms of the pro-mammalia is extremely important. To summarize, it is rendered probable that the earliest forms of mammals were homodont and had two or more series of successional teeth. Then within the mammalian stem the teeth were differentiated, and there arose a great heterodont group with teeth at least of three kinds—incisors, premolars and molars, all successional. From the most anterior premolar arose the canine. Then came the division between the Marsupials and the Placentals, the former tending to suppress the development of the second series of teeth, the latter retaining the second series as far back as the first molar.

We can see an obvious advantage in the line of succession being drawn at the first molar,[1] for upon the molars rested the necessity of complex development, and such development was best effected in permanent crowns.

1. All the so-called "milk molars" plus the so-called "true molars" constitute the *first series.* Beneath one or more of the "true molars" in lower mammals are rudiments of a second series. The *second series* consists therefore of these sub-molar rudiments plus the successional or permanent premolars, incisors and canines.
2. In the stem Marsupials the entire first series persisted and became mainly permanent (non-deciduous); the second series became rudimentary and non-successional with the exception of the fourth upper and lower premolars and possibly one or two other teeth which either replaced or were intercalated between members of the first series. One or more premolars were suppressed and one more molar retained than typical in the Placentals. Thus is explained the apparently atypical dental formula of Marsupials.
3. In the stem heterodont Placentals (excepting the Cetacea and Edentata) the entire first series persisted and all the incisors, canines and premolars remained deciduous. The successional second series persisted as far back as the first molar.
4. In the stem Cetacea the entire first series persisted and the second series became rudimentary and non-successional. The tooth form changed from a heterodont to a homodont type.
5. In the stem Edentates, which also transformed from the heterodont to the homodont type, the first series became rudimentary and the second series persisted in the succession even behind the region of the first molar.

Finally, there is evidence that a primitive succession in the region of the molar teeth, lost in the Marsupials and in the Placentals, was more or less fully retained in the Cetacea and Edentates.

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[1] The law of molar evolution is that complication is most rapid in teeth which are longest in use. Thus the first molar is the most progressive tooth of the true molar series and the last premolar is the most progressive of the premolar series. The apparent exception that the third milk premolar is always an advance type of the third permanent premolar is explained by the fact that the milk premolars are formed to assume the molar function.

Biological Department, Columbia College, April 10, 1893.

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